# THE SUBTRIBE HICKSBEACHIINAE (PROTEACEAE) IN THE AUSTRALIAN TERTIARY

ANDREW C. ROZEFELDS

Rozefelds, A.C. 1992 06 29: The subtribe Hicksbeachiinae (Proteaceae) in the Australian Tertiary. *Memoirs of the Queensland Museum* **32**(1): 195-202. Brisbane. ISSN 0079-8835.

*Wilkinsonia bilaminata* F. Muell., a fossil fruit from deep leads at Gulgong, New South Wales is similar to fruits of extant genera *Athertonia* and *Heliciopsis* (subtribe Hicksbeachiinae: Proteaceae). *Athertonioides* Rozefelds is considered a synonym of *Wilkinsonia*. Fossil evidence of *Wilkinsonia* in the mid-Tertiary demonstrates that the subtribe was more widespread than at present. *Wilkinsonia* is more closely related to *Athertonia*, the north Queensland rainforest endemic, than to the South East Asian genus *Heliciopsis*.□ *Proteaceae, Hicksbeachiinae, Athertonia, Heliciopsis, Wilkinsonia, Athertonioides, fossil fruit, Australia, Tertiary.*

*Andrew C. Rozefelds, Queensland Museum, PO Box 3300, South Brisbane, Queensland, 4101, Australia; present address: School of Botany, University of Melbourne, Parkville, Victoria 3052, Australia; 30 January, 1991.*

Mueller (1879, 1883) described *Wilkinsonia bilaminata* on the basis of woody fruits from deep leads (buried placer deposits) below basalts in the Orange and Gulgong gold mining areas of New South Wales. Mueller (1879, 1883) recorded *W. bilaminata* from Beneree, near Orange at a depth of about 110-130ft and in deep leads at Gulgong at a depth of 140-175ft (Fig. 1). He was unsure of the affinities of *W. bilaminata* but suggested (1879: 170) that it 'may perhaps have belonged to the order of Sapindaceae; but with the material at present available it is impossible to find its exact ordinal position, as no external resemblance indicates any close relationship to existing genera'. The only surviving specimen located is in the Museum of Victoria (NMVP53092) from the Gulgong locality in New South Wales.

Palynological studies of the Home Rule Kaolin Deposit which is part of one of the deep leads in the Gulgong area indicates they are of late early to middle Miocene age (McMinn, 1981). Potassium-Argon dates of $14.8 \pm 1.2$ and $13.8 \pm 1.1$my BP. for basalts that overlie deep leads in this area (Dulhunty, 1971) indicate a minimum mid-Miocene age for this flora.

Fruits from the Oligocene Glencoe locality in central Queensland were placed in a new form genus *Athertonioides* which closely resembles those of the north Queensland endemic *Athertonia*, and South East Asian genus *Heliciopsis*, (both in subtribe Hicksbeachiinae) (Rozefelds, 1990a). Re-examination of topotypic material of *W. bilaminata* F. Muell. from the Gulgong locality also suggests inclusion in Hicksbeachiinae (Fig. 2).

In this paper *W. bilaminata* is redescribed and it's affinities discussed. The status of *Athertonioides* Rozefelds is also re-examined. Fruit anatomy of extant genera *Heliciopsis, Athertonia* and *Hicksbeachia* is also figured and the fossil record of Hicksbeachiinae in Australia is reviewed.

## METHODS AND MATERIALS

To permit comparison with the fossil material, the soft outer exocarp and mesocarp layers of modern fruits were removed. Persistent fibres attached to the stony layer (endocarp) of the fruit were removed with a nylon brush. The endocarp was sectioned with a coping saw and the transverse sections polished with 1200 grit 'wet and dry sandpapers'. The sections were photographed with a Carl Zeiss DRC Stereo Microscope with MC63 camera attachment. Comparative modern Australian material figured in this paper will be donated to the Queensland Herbarium (BRI).

The term endocarp is used here in a descriptive sense and follows that of Sleumer (1955a,b), (Smith & Haas, 1975) and Filla (1926). Johnson & Briggs (1975), however, have concluded that this inner stony layer is part of the mesocarp. The mesocarp consisting of an outer zone of parenchymatous tissue with radial fibres and inner dense hard zone of tangentially oriented fibres.

Silicified fossil material from Glencoe (Queensland Museum locality QML511) is preserved as moulds with little or no internal cellular preservation. Gulgong and other deep leads fruits approach fusanites in appearance, which

suggests they have been subjected to considerable heat and pressure. During fossilization, the more volatile endocarp wall constituents are lost, leaving only the ligneous structure of the fruit. In modern fruits the volatile endocarp wall constituents are still present making comparisons difficult.

## SYSTEMATIC PALAEOBOTANY

### Family PROTEACEAE
### Tribe MACADAMIEAE
### Subtribe HICKSBEACHIINAE

Rozefelds (1990a) erected *Athertonioides glencoensis* for fossil fruits collected from the Glencoe locality in central Queensland. Re-examination of *Wilkinsonia bilaminata* also indicates close affinities with *Athertonia*. It is not warranted to maintain two form genera for fossil *Athertonia*-like fruits and so *Athertonioides* is here reduced to a synonym of *Wilkinsonia*. In his diagnosis of *Wilkinsonia*, Mueller (1879, 1883) drew prominent attention to the flattened nature of the endocarp and the ridging which are features, that are in part, due to compression during fossilization. An emended diagnosis of *Wilkinsonia bilaminata* is provided. The original specimen figured by Mueller (1879: pl. 3, fig. 4a,b) has not been located in the Museum of Victoria, Geological Survey of New South Wales or Australian Museum collections. It seems likely that as the original material was obtained by C.S. Wilkinson (Geological Survey, New South Wales), the figured specimen would have been lodged in their collections, but may have been subsequently lost in the Garden Palace fire, Sydney, 1882 (J. Pickett, pers comm. 1992). A neotype is erected here, which is probably the specimen figured by Mueller (1883: pl. 3).

Geological Survey of New South Wales specimens (MMF31337-31343) from the Newstead Mine, Elsmore, northern NSW have been tentatively compared with *Wilkinsonia* (Pickett et al., 1990). These compressed fruits however lack the reticulate lacunose ornamentation and longitudinal ridges characteristic of this genus. The affinities of these fruits remain unknown.

### **Wilkinsonia** (F. Muell., 1879) emend.

TYPE SPECIES

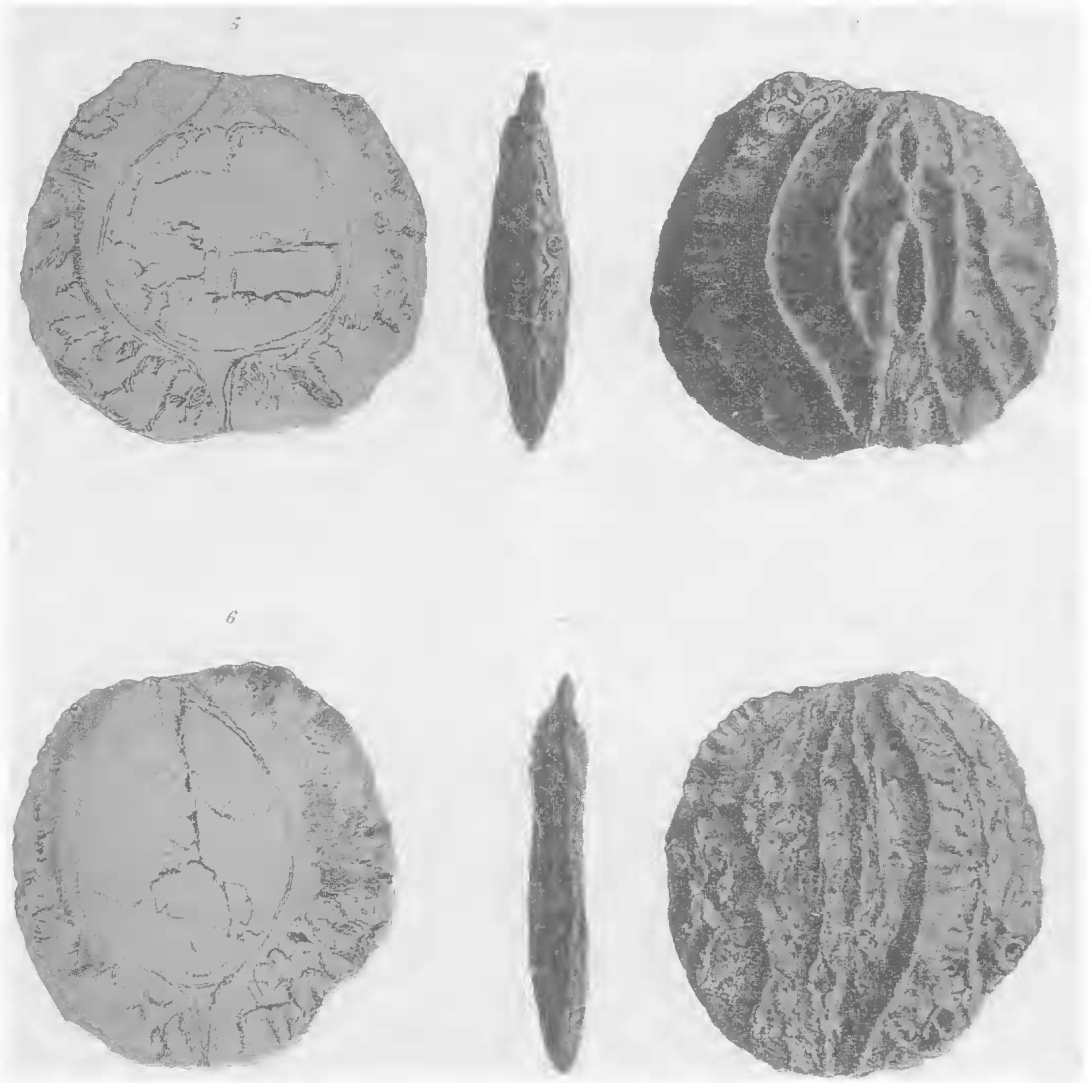
*Wilkinsonia bilaminata* F. Muell., 1879.


FIG. 1. Localities mentioned in text and distribution of modern genera and species of Australian Hicksbeachiinae.

EMENDED DIAGNOSIS

Endocarp indehiscent, variable in shape and size, with variable development of longitudinal ridges, reticulate lacunose surface consisting of irregular depressions. Depressions variable in size. Base of depressions confluent with internal wall of endocarp. Incipient curved longitudinal ridge continuous from apex to base of endocarp. Irregular rows of small depressions between incipient ridge and edge of endocarp. Monolocular.

FIG. 2. Reproduction of Mueller's (1883) original figure of *Wilkinsonia bilaminata*, × 0.7. The specimens were originally illustrated by Mueller at natural size.



**Wilkinsonia bilaminata** (F. Muell., 1879) emend. (Figs 2, 3A-D).

1879. *Wilkinsonia bilaminata* F. Muell., p. 170, pl. 3, fig. 4a,b.
1883. *Wilkinsonia bilaminata* F. Muell., p. 7, pl. 3 (refigured herein).

MATERIAL EXAMINED

NEOTYPE: NMVP53092 (here designated), Black Lead, 140-170ft below basalt, Gulgong, NSW (Fig. 3A-D).

EMENDED DIAGNOSIS

Large round monolocular endocarp, with reticulate lacunose ornamentation consisting of longitudinal ridges with ramifying supporting lateral ridges. Approximate size of endocarp (due to fraying of edges), length 46.3mm, width 45.9mm. A prominent incipient lateral ridge extends from the apex to the base of the endocarp. A broad lateral field occurs between incipient ridge and edge of endocarp with minor accessory lateral ridges and irregular rows of small depressions. Endocarp thinly elliptical in lateral view, although this is due to lateral compression. Multiple irregular rows of depressions and secondary ridges occur between the lateral ridge and the edge of the endocarp. The endocarp wall which is 2-3 mm in thickness, con-

sists of tangentially oriented interweaving fibres. Evidence of radial fibres around lacunae is missing but as these fibres are not strongly lignified they are unlikely to be preserved in fossil material.

**Wilkinsonia glencoensis** (Rozefelds) comb. nov. (Fig. 4A-C).

1990a. *Athertonioides glencoensis* Rozefelds, pp. 123-4, fig. 3,A- C,D(left figure), E,H.

MATERIAL EXAMINED

Holotype, QMF17212 and additional specimens from the mid-Tertiary Glencoe locality (QML511), near Capella, CQ, figured by Rozefelds (1990a).

DIAGNOSIS

Endocarp variable in size, broad to suboval or rounded in outline, with prominent reticulate lacunose ornamentation, ridging poorly developed, length 36-43mm; width 25-34mm, height 14-21mm. A narrow lateral field with multiple irregular rows of depressions occurring between incipient ridge and edge of endocarp. Endocarp wall thick, but ligneous structure not preserved.

REMARKS

The two *Wilkinsonia* species differ in the width of the lateral field between the incipient ridge and edge of the endocarp. In *W. bilaminata* this zone is broad while in *W. glencoensis* and closely related modern genera of the Hicksbeachiinae, it is narrow. This broad field in *W. bilaminata* is reflected by the presence of multiple irregular rows of small depressions with accessory ridges between the incipient ridge and edge of the endocarp. *W. bilaminata* also appears to possess more pronounced longitudinal ridges than *W. glencoensis,* but these ridges along with the flattened appearance of the endocarp are in part, due to compression.

## ENDOCARP MORPHOLOGY OF EXTANT GENERA IN THE HICKSBEACHIINAE

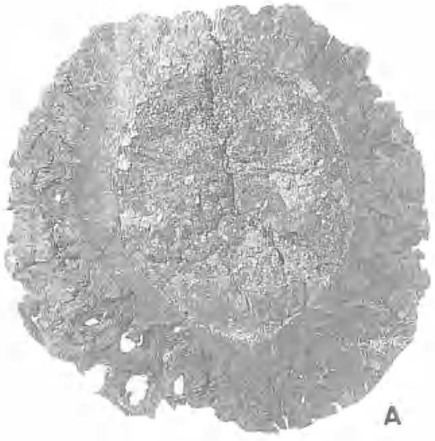
The endocarps of *Wilkinsonia* are strongly lignified which helped facilitate fossilization. The endocarp wall in *Heliciopsis* and *Athertonia* consists of tangentially and radially oriented fibres. In *Athertonia* the tangentially oriented fibre bands are numerous and diffuse while in *Heliciopsis artocarpoides*, the endocarp wall is thin and there are areas of lignified parenchyma interspersed around the tangentially oriented fibres (Fig. 4F, J). The radial fibres in *Athertonia* and *Heliciopsis* tend to be perpendicular to the outside edge of the endocarp. In *Heliciopsis* the radial fibres around the lacunae are variously oriented, and sometimes oblique to the endocarp wall (Fig. 4F-G,J-K).

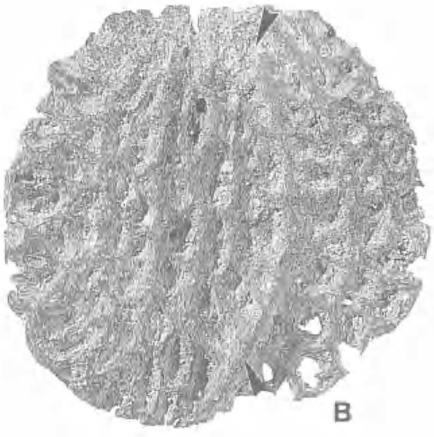
In *H. artocarpoides* (Elm.) Sleumer the reticulate lacunose ornamentation is less developed and the ridging is less prominent than in *Athertonia* (Fig. 4H-I). Most species of *Heliciopsis* conform to the endocarp morphology in *H. artocarpoides* although material from Sumatra, figured as *Heliciopsis* sp. and tentatively compared with *H. incisa* by Sleumer (1955a:191,194) resembles *Athertonia* in having more thickly walled and more strongly ornamented endocarps. The endocarp wall of *Heliciopsis* sp. also lacks the internested lacunae typical of *H. artocarpoides* (Sleumer, 1955a).

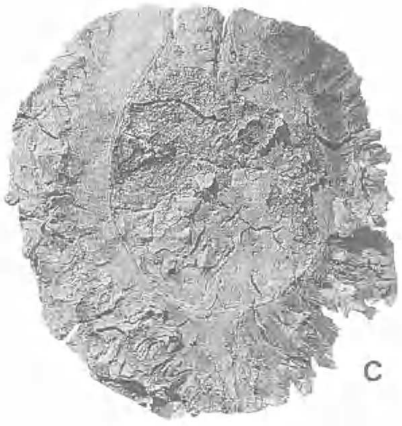
*Hicksbeachia* is the only other genus of this subtribe in Australia with two allopatric species in eastern Australia (Weston, 1988). The endocarp of *Hicksbeachia pinnatifolia* lacks reticulate lacunose ornamentation. In the specimens of *Hicksbeachia* available there is not a clear separation between the inner ligneous (endocarp) and outer fleshy mesocarp. The endocarp in *Hicksbeachia*, in transverse section has prominent vascular bundles that are oriented longitudinally, (absent in *Heliciopsis* and *Athertonia*) and poorly lignified radial fibres extend from the outer edge of the endocarp into the fleshy mesocarp (Filla, 1926; Fig. 4L, M). Similarly in *Athertonia* and *Heliciopsis* radial fibres extend from the endocarp into the mesocarp, with persistent radial fibres evident around the lacunae. The endocarp (inner mesocarp of Weston, 1988) in *Hicksbeachia* consists of tangentially oriented fibres and lignified parenchyma.

The remaining genera in the Hicksbeachiinae; *Virotia* from New Caledonia lacks reticulate lacunose ornamentation of the endocarp while the fruit morphology of *Malagasia* from Madagascar is unknown (Johnson & Briggs, 1975; Virot, 1968).

FIG. 3. A-D, *Wilkinsonia bilaminata*. F. Muell. (NMVP53092). A,C, Internal view of endocarp wall × 1.2. B,D, External views of endocarp wall. Note prominent lacunae and the position of the incipient ridge indicated by arrows and wide lateral field × 1.3. E-F, *Athertonia diversifolia* (C.T. White) L. Johnson & B. Briggs × 1.5. E, Internal view and F, external view of endocarp wall.

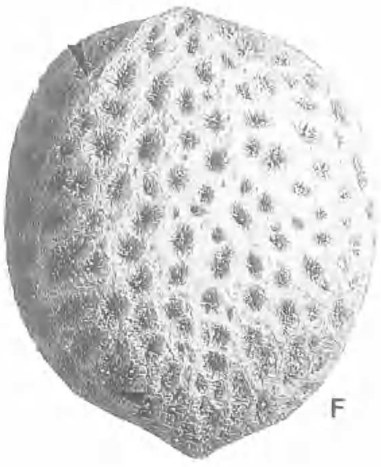

A


B


C


D


E


F

## CONCLUSION

The large endocarp, incipient ridge extending from the apex to the base and prominent reticulate ornamentation and arrangement of tangential fibres in *Wilkinsonia* strongly suggest affinities with genera in the subtribe Hicksbeachiinae (Sleumer, 1955 a,b; Rozefelds, 1990a). These external endocarp features are shared with *Athertonia* and *Heliciopsis* but are absent from *Hicksbeachia* and *Virotia*.

*Wilkinsonia* is more closely related to *Athertonia* than to *Heliciopsis*. In *Heliciopsis* the depressions on the endocarp wall tend to consist of internested small lacunae while in *Athertonia* and *Wilkinsonia* they tend to be separate and not internested. The endocarp wall in *W. bilaminata* is strongly ornamented, consists of separate lacunae surrounded by tangentially oriented fibres. The endocarp wall is relatively thin and the simple perpendicularly oriented lacunae in *Wilkinsonia* are similar to *Athertonia*. The internal ligneous structure of *W. glencoensis* is not preserved although the endocarps are thick and woody, have perpendicularly oriented lacunae as in *Athertonia* and differ from the relatively thin walled endocarps of *Heliciopsis* (Rozefelds, 1990a) (Fig. 4).

The fossil distribution of *Wilkinsonia* demonstrates that the subtribe Hicksbeachiinae was more widespread than at present (Fig. 1). *Wilkinsonia* is most closely related to *Athertonia* which is presently restricted to rainforest communities on the Atherton Tablelands of north eastern Queensland. Similarly the allopatric distribution of *Hicksbeachia*, and restriction to widely separated mesic rainforest communities is suggestive of a more widespread range for this genus during the Tertiary, which may have encompassed much of eastern Australia (Fig. 1). The close relationship of *Wilkinsonia* to *Athertonia*, and the presence of *Elaeocarpus* (Rozefelds 1990b) in this flora suggests that the Gulgong area during the mid-Miocene was dominated by rainforest. The taxonomic diversity and structure of these mid-Tertiary rainforests will be more fully understood when the affinities of the remaining fruits and seeds described by Mueller (1879, 1883) are recognized. This will only be achieved by the concurrent study and description of fruits and seeds of the contemporary Australian flora.

## ACKNOWLEDGEMENTS

The Jabatan Perhutanan Herbarium, Sandakan, Sabah, Malaysia provided material of *Heliciopsis artocarpoides* (SAN 28114) for study. *Athertonia* and *Hicksbeachia* fruits were supplied by T. Irvine and P. Weston respectively. P. Jell and A. Drinnan gave helpful advice and comments on this paper. The Museum of Victoria provided funding for my visit, allowing access to collections and photographed the original plates from Mueller's papers. Most of the remaining photographs were taken by the photography section at the Queensland Museum. Information and/ or access to collections was provided by R. Jones (Australian Museum), E. Thompson (Museum of Victoria) and J. Pickett (Geological Survey of New South Wales).

## LITERATURE CITED

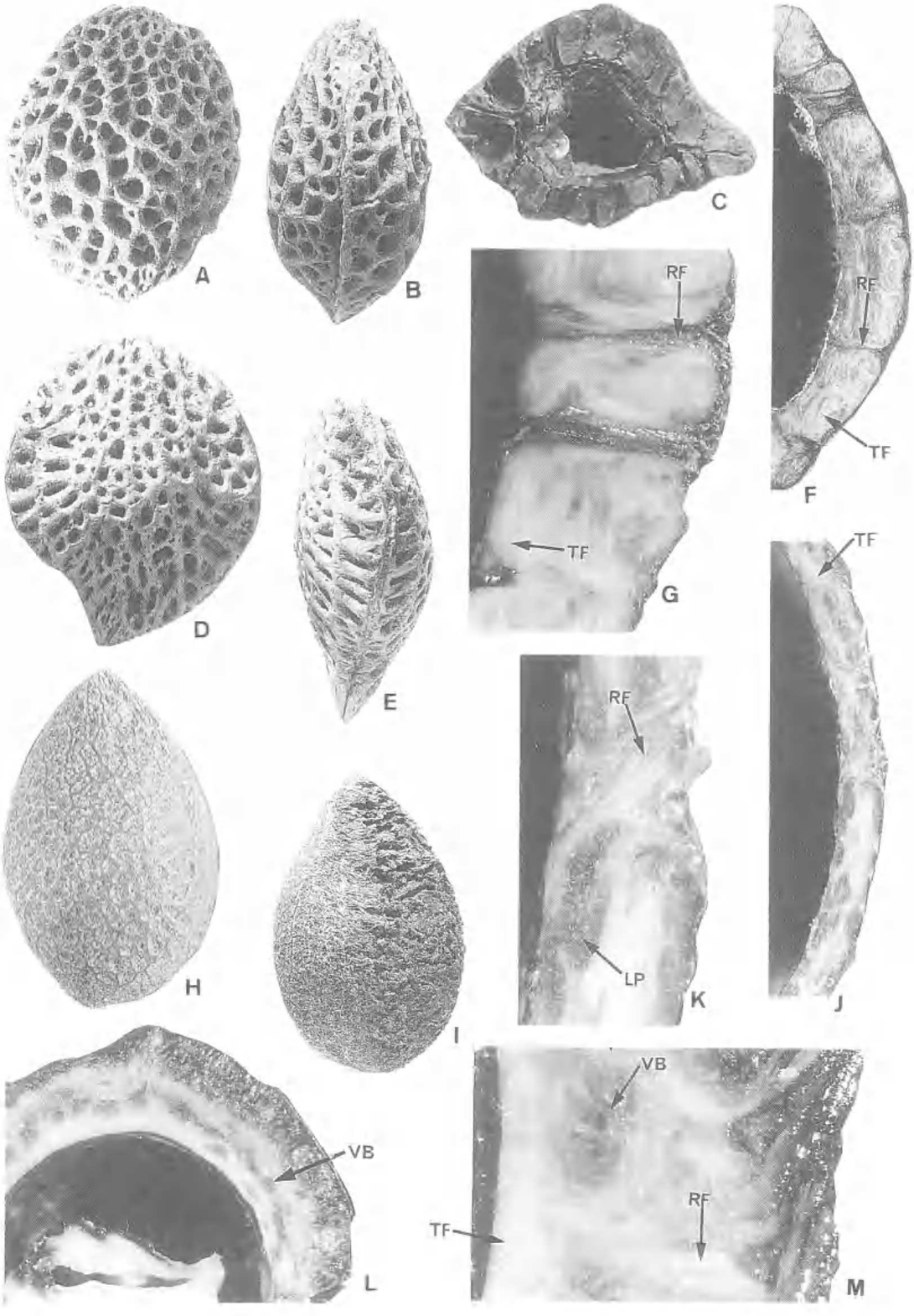
DULHUNTY, J.A. 1971. Potassium-Argon dates and their significance in the Ilford-Mudgee-Gulgong region. Journal and Proceedings of the Royal Society of New South Wales 104: 39-44.

FILLA, F. 1926. Das pericarp der Proteaceae. Flora 120: 99-142.

JOHNSON, L.A.S. & BRIGGS B.G. 1975. On the Proteaceae - the evolution and classification of a southern family. Botanical Journal of the Linnean Society of London 70: 83-182.

McMINN, A. 1981. A Miocene microflora from the Home Rule Kaolin Deposit. Quarterly notes of the Geological Survey of New South Wales 43: 1-4.

FIG. 4. A-C, *Wilkinsonia glencoensis* (Rozefelds). A, QMF17212, external view of endocarp note prominent simple lacunae × 1.2. B, lateral view of same specimen showing narrow lateral field between edge of endocarp and lateral ridge × 1.2. C, QMF17211, natural transverse section of exoocarp × 1.7. D-G, *Athertonia diversifolia*. D. External views of endocarp × 1.1. E, Lateral view of same specimen showing narrow lateral field × 1.1. F- G, Transverse section of endocarp wall showing strongly lignified tangentially oriented fibres (TF) and poorly lignified radially oriented fibres (RF) F × 2.3, G × 6.7. H- K, *Heliciopsis artocarpoides* (SAN 28114). H, External view of endocarp showing internested lacunae × 1.7. I, lateral view of same specimen showing internested lacunae of the endocarp wall and fine radial fibres that extend into mesocarp, the thin exocarp wall has flaked away from the mesocarp, × 1.5. J-K, transverse section of endocarp wall showing radial fibres (RF), transverse fibres (TF) and ligneous parenchyma (LP), J × 5.8, K × 20.5. L-M, Transverse sections of *Hicksbeachia pinnatifolia* F. Muell., endocarps showing vascular bundles (VC), radial fibres extending from near the mid-region of the endocarp extending into the mesocarp; tangential fibres occur along inner wall of endocarp, L × 4.3, M × 17.0.


A
B
C
RF
RF
F
TF
D
E
TF
G
TF
J
RF
LP
K
H
I
VB
L
VB
RF
TF
M

MUELLER, F. Von 1879. Appendix D. Deseriptive notes on the Tertiary flora of New South Wales. Pp. 169-72. (Annual Report, 1878, Mines Department, New South Wales).

1883. 'Observations on new vegctable fruits of the auriferous drifts Dec.2.' (Geologieal Survey of Victoria; John Ferres, Government Printer: Melbourne). 23pp.

PICKETT, J.W., SMITH, N., HILL, R.S., MACPHAIL, M.K. & HOLMES, W.B.K. 1990. A stratigraphic evaluation of Ettingshausen's New England Tertiary localities. Australian Journal of Earth Seiencs 37: 293-303.

ROZEFELDS, A.C. 1990a. A mid Tertiary rainforest flora from Capella, central Queensland. Pp. 123-136. InDouglas, J.G. & Christophel, D.C. (eds), 'Proceedings, Third International Organization of Palaeobotany, 1988'. (A-Z Publishers: Melbourne).

1990b. 'A taxonomie study of extant and fossil fruits of the genus Elaeocarpus (Elaeoearpaeeae) in Australia and New Zealand'. (Unpublished Honours Thesis, Botany Department, University of Adclaide).

SLEUMER, H. 1955a. Proteaceae. Flora Malesiana (1)5: 147-206.

1955b. Studies in Old World Proteaeeae. Blumea 8: 2-95.

SMITH, A.C. & HAAS, J.E. 1975. Studies of pacific island plants. XXIX. *Bleasdalea* and related genera of Proteaceae. Ameriean Journal of Botany 62(2):133-147.

VIROT, R. 1968. Proteaeées. In Aubréville, A. (ed.), 'Flora de la Nouvelle Calédonie et depéndances.' 2: 1-254. (Muséum National d'Histoire Naturelle: Paris).

WESTON, P.H. 1988. A revision of *Hicksbeachia* (Proteaceae). Telopea 3(2): 231-239.